NOTES ON THE MUSHROOM BODIES OF THE INVERTEBRATES.

A PRELIMINARY PAPER ON THE COMPARATIVE STUDY OF THE ARTHROPOD AND ANNELID BRAIN.

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MUSHROOM bodies, fungiform bodies, pedunculated bodies, are synonyms that have been applied to certain peculiar structures found in the insect brain. These bodies were first discovered by Dujardin.[1] Although rediscovered by Leydig[2] and Rabl-Rueckhard,[3] yet aided by osmic acid, the microtome and staining fluids, Dietl[4] was the first to give a complete description of the whole organ. Thanks to the researches of more recent investigators, it is now well known that the mushroom bodies occur in all classes of insects, and that they reach their highest development in the *Hymenoptera*. Dietl,[4] Berger,[5] and Viallanes[6] have found in the *Decapod* brain structures which they consider homologues of the mushroom bodies of the *Hexapod* brain. Kenyon,[7] as the following quotation shows, thinks all of these men are mistaken. "Special swellings found on the brains of certain of the Crustacea have been compared to them (the mushroom bodies), but it is seriously doubted, I think, whether such swellings or cellular heaps are properly to

[1] Dujardin, "Mémoire sur le Systeme nerveux des Insects," *Ann. Sci. Nat.* Ser. 3, tome xiv, pp. 195 *et seq.*, Pl. IV. 1850.

[2] Leydig, Vom Bau des thierischen Körpers. pp. 232 *et seq.* 1864.

[3] Rabl-Rueckhard, "Studien über Insektengehirne," *Reichert und Du Bois-Raymond's Archiv. f. Anat* pp. 488, 489. 1875.

[4] Dietl, "Die Organisation des Arthropodengehirns," *Zeit. f. wiss. Zool.* Bd. xxviii, pp. 488–517. 1876.

[5] Berger, "Untersuchungen über den Bau des Gehirns und der Retina der Arthropoden," *Arb. Zool. Inst. zu Wien.* Bd. i, Heft 2. 1878.

[6] Viallanes, H., "Étude Histologique et Organologique sur les Centres Nerveux et les Organs des Sens des Animaux Articules," *Ann. Sci. Nat. Zool. et Pal.* Tome xiv, pp. 405–455, Pls. X, XI. 1893.

[7] Kenyon, F. C., "The Brain of the Bee," *Journ. of Comp. Neurology.* Vol. vi, pp. 133–210, Pls. XIV–XXII. 1896.

be homologized directly with them. In neither Retzius' figure of the brain of *Astacus fluviatalis*, nor in Bethe's figures of the brain of *Carcinus moenus*, can I find cells having the relations and the appearance of those I find in the bee. I have noticed

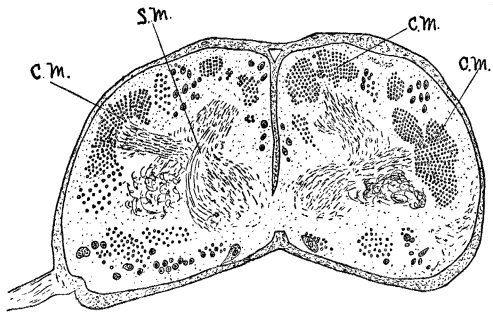

FIG. 1. — Section through the mushroom bodies of *Cecropia* larva.

nothing resembling the structures in Isopods or Amphipods, nor have I found indications of them in the brains of *Pauropus*, *Polyxenus*, *Scolopendrella*, *Lithobius*, nor even in several forms of *Thysanura* that I have examined. If cells homologous with those filling the cup-like calyx of the mushroom bodies of the bee are at all present in these forms, they are so undifferentiated as to be indistinguishable from the general mass of cells about them."

More recently Hamaker [1] has homologized certain groups of cells found in the brain of *Nereis* with the Hexapod mushroom

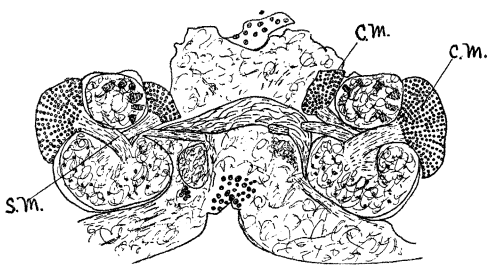

FIG. 2. — Section through the brain of *Cambarus*.

bodies. He bases this conclusion upon the following facts: (1) the cells of that type are confined to the brain; (2) they

[1] Hamaker, J. J., "The Nervous System of *Nereis virens* Sars," *Bull. Mus. of Comp. Zool. at Harvard College*. Vol. xxxii, No. 6. 1898.

are intimately connected with the neuropil; (3) they have small nuclei, and very little cytoplasm; (4) they are arranged in rows radiating from the neuropil.

While now at work upon a comparative study of the Arthropod and Annelid brain, several preparations have been examined which throw light upon the distribution of the mushroom bodies. Since it will be some time before these studies can be completed, certain discoveries bearing directly upon the distribution of the mushroom bodies are described in this preliminary paper.

The author does not consider this the place to record the bibliography, nor to discuss the technique, nor to acknowledge

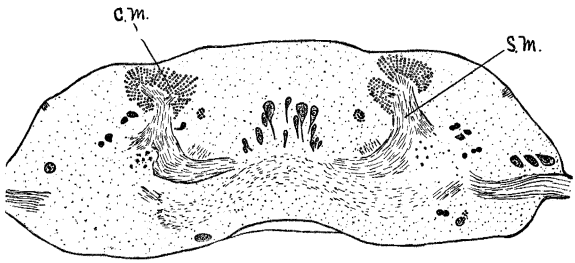

FIG. 3. — Section through the brain of *Nereis*.

his indebtedness to those who have in any way aided him in these studies. All such information will be given in the final paper.

The mushroom bodies are composed of two factors, cells and fiber tracts. The cells are minute bodies having small nuclei and almost no cytoplasm. In this respect they resemble Deiter's corpuscles of the vertebrate brain. Compact masses of these cells crown each stalk. In these nidi the cells are arranged in rows which radiate from the top of each stalk. In each half of the brain the principal fibers of the mushroom bodies are collected in a stalk which lies, more or less erect, in a plane which cuts the longitudinal axis of the brain nearly at right angles. The top of each stalk may be either unbranched or bifurcated or ramosely branched. The lower portion of the stalk usually gives rise to two branches, one passing outwards (laterad) and the other inwards (mesad).

The preparations at my disposal make possible the demonstration of these bodies not only in the Hexapods (Fig. 1), but also in the Decapods (Fig. 2), and in the *Xiphosura*, and in cer-

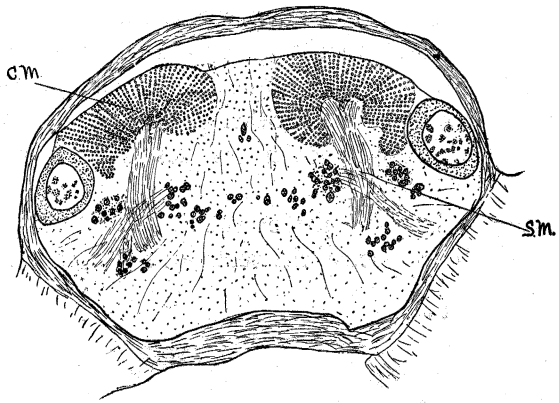

FIG. 4. — Section of *Polynöe*.

tain *Polychaeta* (Figs. 3–5), etc. In the *Polychaeta* the stalk seems to be unbranched (Fig. 5), although in *Nereis* (Fig. 3) and *Polynöe* (Fig. 4) there is a slight indication of a bifurcation; in the Hexapods (Fig. 1) and the Decapods (Fig. 2) it is bifur-

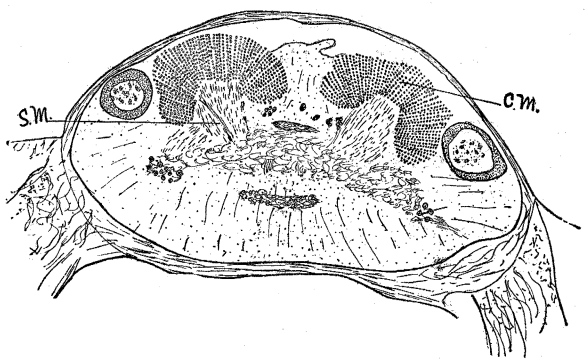

FIG. 5. — Section of *Lepidonotus*.

cated, while in *Limulus* (Fig. 6) it is ramose. Indeed, in *Limulus* it is so much branched that it simulates, in structure, the vertebrate cerebellum.

At present it is not possible to state whether these mush-

room bodies occur in all *Polychaeta* or not; but it is possible to assert that they exist in *Nereis*, *Lepidonotus*, and *Polynöe*. Nor is it possible to aver their existence in all Crustacea; but it is certain that they occur in *Cambarus* and *Limulus*. Both of these questions will be considered at length in the final paper to which is relegated a discussion of several fiber tracts connected with the mushroom bodies.

It is thought that sufficient facts and figures have been given to demonstrate that the mushroom bodies occur in the Hexapods, Decapods, *Xiphosura*, and certain *Polychaeta*. In each case these

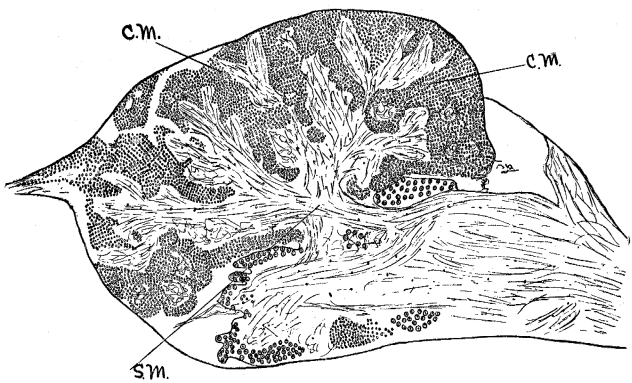

FIG. 6. — Sagittal section through the brain of *Limulus*.

bodies lie in the front portion of the supra-oesophageal ganglion. Is it not logical to conclude that the front portions of these brains are homologous? This statement runs counter to the generally accepted view. Goodrich,[1] who has recently investigated this question, does not think that the homologue of the Annelid prostomium, with its archicerebrum, occurs in either the insects or the Crustacea. But, since the mushroom bodies constitute the major portion of the protocerebrum of Hexapods and Decapods, and since the mushroom bodies occur also in the archicerebrum of certain *Polychaeta*, it follows that at least the major portion of the protocerebrum of the insects and the

[1] Goodrich, E. S., "On the Relation of the Arthropod Head to the Annelid Prostomium," *Quart. Journ. Micr. Sci.* Vol. xl, pt. ii, new series, pp. 247–268, 12 figs. 1897.

Crustacea is the homologue of the archicerebrum (supra-oesophageal ganglion) of the polychaete annelids.

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September 14, 1898.

REFERENCE LETTERS.

C.M., cells of the mushroom bodies.
S.M., stalk of the mushroom bodies.

All figures were drawn with a camera. Figures 2 and 6 are drawn to the same scale. Figures 3, 4, and 5 are drawn to the same scale, but are enlarged more than 2 and 6. Figure 1 is enlarged more than any of the others.